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DO RINGTAILED LEMURS EXHIBIT A SKEWED BIRTH SEX RATIO DEPENDING ON SOCIAL AND ENVIRONMENTAL CONDITIONS? A PRELIMINARY ANALYSIS OF A WILD POPULATION

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ABSTRACT In a 13-year study, we examined the birth sex ratio (BSR) of wild ringtailed lemurs at Berenty Reserve in Madagascar. Their BSR represented an equal sex ratio at the population level, irrespective of population change. High-ranking females did not always overproduce sons or daughters. In newly formed groups, females did not always overproduce daughters, and the BSR of young females was similar to an equal sex ratio. Thus, our data do not support the Trivers–Willard, local resource competition–population, or local resource enhancement hypotheses. Only one significant skewed BSR was observed: low-ranking females in medium-sized groups overproduced sons. This finding may support the local resource competition–individual hypothesis, but does not do so robustly.

Key Words: *Lemur catta*; Birth sex ratio; Local resource competition.

INTRODUCTION

Currently, controversy exists as to whether female primates exhibit skewed birth sex ratios (BSRs) under varying social and environmental conditions. Four hypotheses have been proposed with reference to skewed BSRs in primates: the Trivers–Willard hypothesis (Trivers & Willard, 1973), the local resource competition (LRC)–population hypothesis (Clark, 1978), the local resource competition (LRC)–individual hypothesis (Silk, 1983), and the local resource enhancement (LRE) hypothesis (Nunn & Pereira, 2000).

Although each of these hypotheses is supported by several data sets, considerable research exists that does not support any of them. For example, Brown (2001) could not find a consistent pattern between maternal rank and BSR in 14 primate population data sets (10 species), and Brown & Silk (2002) concluded that the null hypothesis, which states that the maternal dominance rank is unrelated to BSR, could not be rejected on the basis of a meta-analysis. In contrast, Schino (2004) reported that the relationship between BSR and dominance rank was affected

by the level of resource availability and degree of sexual dimorphism on the basis of another meta-analysis of BSR variations in 18 primate species.

We performed a long-term study of a wild ringtailed lemur (*Lemur catta*) population at Berenty Reserve in southern Madagascar (Koyama et al., 2005; Takahata et al., 2006). Ringtailed lemurs form matrilineal/female-bonded groups ranging from 3 to 28 individuals (Koyama et al., 2002). Severe within- and intergroup female competition is frequently observed. Thus, ringtailed lemurs may be a good model species for evaluating socioecological hypotheses.

In this report, we analyzed 13 years of data obtained from observations of this population to determine whether female ringtailed lemurs exhibit a skewed BSR. Our data did not support the Trivers–Willard, LRC–population, or LRE hypotheses. Only one significant skewed BSR was observed, with low-ranking females in medium-sized groups overproducing sons. However, our data do not support the expectation that high-ranking females would overproduce daughters. Thus, our data may lend some limited support to the LRC-individual hypothesis, but this could not be considered robust.

STUDY SUBJECTS AND METHODS

We used 60 group-years of birth data obtained from observations of wild ringtailed lemurs at Berenty Reserve in southern Madagascar between 1989 and 2001 (Table 1). Females aged 3 years or older and primiparous 2-year-old females were considered adults. They were ranked on the basis of approach–retreat interactions while feeding and drinking and submissive vocalizations (spat-calls; Koyama et al., 2005). The relative ranks of all adult females were calculated for each study year using a formula that indexed the highest ranking female as 100% and the lowest ranking female as 0%. These were as follows:

$$\text{Relative rank of a lemur (\%)} = (N - R) \div (N - 1) \times 100$$

N: number of adult females in the group.

R: rank of the individual among adult females.

Table 1. Study groups and number of years of observation

Group	Years of observation
CX	8
C1	12
C2	8
C2A	5
C2B	5
T	4
T1	9
T2	8
HSK	1
Total	60

Group size influenced the reproductive parameters of the females in the study population (Takahata et al., 2006). The birth rate and number of surviving infants per adult female generated an inverted U-shaped curve when plotted against group size/number of adult female group members. The study groups were divided into three categories on the basis of the number of adult females in each group: large (8–9 adult females), medium (4–7 adult females), and small (2–3 adult females). The females in each size group were then classified into three rank categories: high (relative rank = 66.8%–100%), middle (33.4%–66.7%), and low (0%–33.3%). Statistical analyses were performed using Excel 2003 (Microsoft, 2003), Statistica (StatSoft Inc., 1999), and R Ver. 2.8.1 (The R Foundation for Statistical Computing, 2008). The level of significance used was $p < 0.05$, and all tests were two-tailed.

RESULTS

I. Pooled Data from All Study Groups

Of 248 infants born between 1989 and 2001, 30 infants disappeared (probably died) immediately after birth, and their sex was unidentified. Excluding these, 113 males and 105 females were identified (Table 2). No population-level bias in BSR existed relative to an equal sex ratio (binomial test, $p > 0.6$). Infant mortality within 1 year after birth was 32.1% for males and 25.3% for females; this difference was not significant ($\chi^2 = 1.19$, $df = 1$, $p > 0.2$).

Of the 58 adult females, the age of 36 females was known. No consistent association was observed between BSR and the age of these females [one-way ANOVA, $F(10, 105) = 0.945$, $p > 0.4$; Fig. 1].

The non-infant population increased from 63 to 82 lemurs between 1989 and 1999. No linear correlation existed between the proportion of male offspring and population size during these 11 years ($n = 11$, $r = 0.0143$, $p > 0.9$; Table 2).

Excluding Group HSK, which was observed for only 1 year, no significant difference in BSR was observed among the remaining seven study groups [$F(7, 210) = 1.389$, $p > 0.2$; Table 3]. Of these groups, Troop CX, C2B, and T2 were newly formed during the study period; they were believed to have been founded by individuals expelled from their original groups by intense and

Table 2. Birth sex ratio (BSR) in all study groups by year

	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	Total
Male infants	6	8	11	7	7	11	14	9	9	11	7	10	3	113
Female infants	4	9	8	4	2	8	9	10	12	8	14	13	4	105
Total	10	17	19	11	9	19	23	19	21	19	21	23	7	218
p	>0.7	1	>0.6	>0.5	>0.1	>0.6	>0.4	1	>0.6	>0.6	>0.1	>0.6	1	>0.6
Non-infant population	63	49	58	73	84	75	81	81	93	100	82	-	-	-

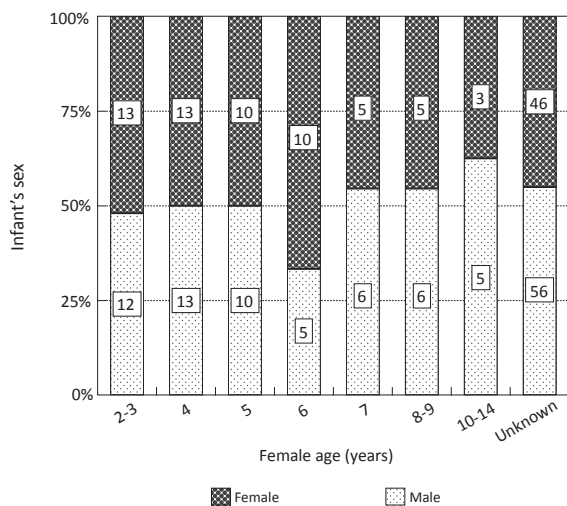


Fig. 1. Female age and birth sex ratio (BSR).

Table 3. The birth sex ratio (BSR) of each study group for all years

Group	C1	CX	C2	C2A	C2B	T	T1	T2	Total
Male	37	9	19	7	0	9	22	10	113
Female	27	9	11	11	5	11	20	11	105
Total	64	18	30	18	5	20	42	21	218
<i>p</i>	>0.2	1	>0.1	>0.3	>0.05	>0.8	>0.7	1	>0.5

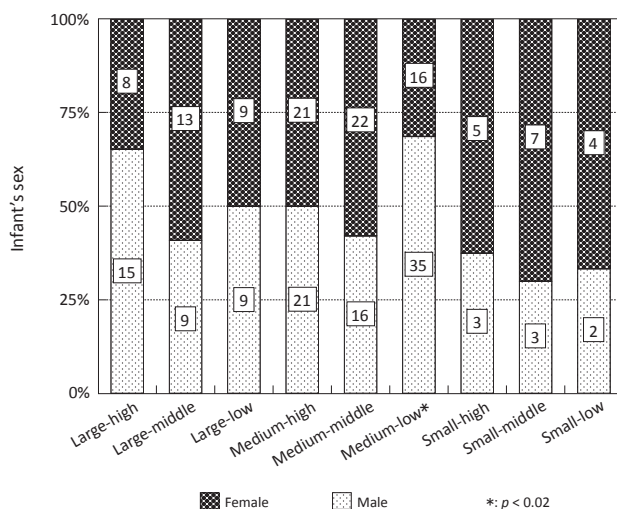


Fig. 2. Birth sex ratio (BSR) among female rank-categories for each group size.

*: Low-ranking females in medium sized groups bore more males than females (binomial test, $p < 0.02$).

persistent aggression (i.e., the “targeting behavior” described by Vick & Pereira, 1989). Nineteen males and 25 females were born to these groups, with no significant difference from an equal sex ratio (binomial test, $p > 0.4$). Although all infants born in Troop C2B between 1997 and 2001 were females, the BSR was still not significantly different from an equal sex ratio ($p = 0.0625$).

II. Group Size and Female Rank

Fig. 2 shows the BSRs of the female rank-groups in the large-, medium-, and small-sized groups. Females in small groups tended to bear more daughters than those in large and medium groups, but this difference was not significant [$F(2, 215) = 1.91$, $p > 0.1$].

Also, no significant difference in BSR was observed among the female rank categories in large groups [$F(2, 60) = 1.354$, $p > 0.2$; Fig. 2]. High-ranking females tended to bear more sons than daughters, but this difference was not significant (binomial test, $p > 0.2$). Similarly, no significant difference in BSR was noted among the female rank-categories in small groups [$F(2, 21) = 0.495$, $p > 0.9$].

However, a significant difference in BSR was detected among the female rank-categories in medium-sized groups [$F(2, 128) = 3.506$, $p < 0.04$]. In particular, low-ranking females tended to bear more sons than daughters (binomial test, $p < 0.02$; Fig. 2).

DISCUSSION

I. Does Maternal Rank Affect the BSR within a Wild Group of Ringtailed Lemurs?

Whether maternal rank is associated with BSR has been particularly controversial. Four hypotheses have been proposed to explain skewed BSRs in primates. The Trivers–Willard hypothesis predicts that dominant females overproduce sons (Trivers & Willard, 1973). This hypothesis is supported by data from several studies (e.g., Meikle et al., 1984; Paul & Kuester, 1990). The local resource competition (LRC)–population hypothesis predicts that when LRC increases, females should overproduce the dispersing sex (e.g., males in female philopatric species; Clark, 1978). The local resource competition (LRC)–individual hypothesis predicts that dominant females overproduce offspring of the philopatric sex because they can support such offspring (Silk, 1983). This hypothesis is supported by data from several studies (e.g., Simpson & Simpson, 1982). The local resource enhancement (LRE) hypothesis proposes that when one sex of offspring “repays” the costs of reproduction by providing benefits to the mother, this sex should be overproduced under appropriate conditions (e.g., new-group formations, within-group aggressions; Nunn & Pereira, 2000).

However, considerable data do not support any of these hypotheses. For example, Brown & Silk (2002) pointed out that a skewed BSR could be the product of stochastic variation in small samples in their meta-analysis of 35 data sets from

15 species in 23 populations. In contrast, Schino (2004) stressed that purely stochastic processes are unlikely to explain the variation in primate BSRs. Thus, the causes of skewed BSRs remain an open question for primatologists.

Nunn & Pereira (2000) analyzed the demographic data of ringtailed lemurs at the Duke University Primate Center to examine the Trivers–Willard, LRC-individual, LRC-population, and LRE hypotheses. However, they found no support for the Trivers–Willard or LRC-individual hypotheses and suggested that LRC interacted with LRE to explain offspring sex ratios in this population.

In this study, high-ranking female wild ringtailed lemurs did not always overproduce sons or daughters, contrary to the expectations of the Trivers–Willard and LRC-individual hypotheses. In addition, no significant correlations were observed between group size and BSR or between female age and BSR. Only one significant skewed BSR was identified, and this was for low-ranking females in medium-sized groups. These females overproduced sons, which could be explained by the prediction of the LRC-individual hypothesis that low-ranking females would produce fewer female offspring, as daughters would be disadvantaged by within-group competition (Nunn & Pereira, 2000). However, the present data do not support the expectation that high-ranking females would overproduce daughters. Thus, our data may support the LRC-individual hypothesis, but this support is not robust.

Several points must be considered when accounting for our inconclusive results. As female rank order in lemurs is unstable compared with those found in cercopithecoid primates (Koyama et al., 2005), high-ranking females cannot afford to use their good condition to skew the BSR. Additionally, several studies have pointed out that the timing of mating relative to ovulation may be important in skewing BSRs (e.g., Watson et al., 1996). However, such a mechanism is unlikely for female ringtailed lemurs because the period of sexual receptivity is extremely limited, with a duration of only a few hours (Jolly, 1967; Koyama, 1988). Also, our sample size was small, giving the possibility of stochastic variation (see Fig. 1 of Brown & Silk, 2002). Further long-term studies are needed to clarify this issue.

II. Does a Skewed BSR Exist at the Population Level?

The intensity of LRC among female primates could be correlated with biased BSRs at the population level. In particular, a male-biased BSR has been reported for prosimian species, which may ultimately result from female LRC (Clark, 1978). Johnson (1988) analyzed data from 15 genera of primates and found that male-biased BSRs tended to occur more often in genera with female philopatry than in those with male philopatry. Watson et al. (1996) analyzed BSR bias in 13 captive prosimian groups and concluded that male-biased BSRs were found in nongregarious, but not in gregarious, species. They proposed that the greater duration of sexual receptivity for nongregarious compared to gregarious females was a possible mechanism for the male BSR bias.

Nunn & Pereira (2000) analyzed a database of ringtailed lemurs at the Duke University Primate Center. They pointed out that in the LRE hypothesis of “delayed benefits,” “philopatric offspring (females in the ringtailed lemur society) serve their

mothers as cooperative partners later in life.” They considered LRE effects to modulate BSR among female ringtailed lemurs and suggested that overproduction of daughters occurs among three types of females: founders of new groups, top-ranking females under conditions of maximal nutrition, and young females that experienced targeted aggression around the mating season.

Silk & Brown (2008) analyzed a large primate data set of 217 samples representing 102 species and 45 genera. They reported that no relationship was observed between BSR and sexual size dimorphism and that in primate groups that do not breed cooperatively, dispersal patterns are linked to BSR, as predicted by the LRC model. A female-biased BSR tends to occur in species in which females disperse, an unbiased BSR occurs in species in which both sexes disperse, and a male-biased BSR occurs in species in which males disperse. Also, cooperatively breeding species (e.g., callitrichids) show a male-biased BSR, as predicted by some forms of the LRE model. They concluded that LRC and LRE shape primate BSRs.

In this study, the BSR of wild ringtailed lemurs was not different from an equal sex ratio at the population level. This finding does not conform to the conclusion drawn by Silk & Brown (2008) that species in which males disperse tend to show a male-biased BSR. Our data tend to agree with the deductions of Watson et al. (1996) stating that gregarious prosimian species do not show a male-biased BSR. BSR was also unaffected by population changes in the study population. These results do not comply with the LRC–population hypothesis, which predicts a population-level male bias in species with male dispersal, particularly when competition increases (Nunn & Pereira, 2000). Furthermore, the females of newly formed groups did not always overproduce daughters in the study population. High-ranking females in large- and medium-sized groups also did not overproduce daughters, and the BSRs of young females were similar to or equal to 1. Thus, our data do not always agree with Nunn & Pereira’s (2000) arguments about LRE effects or Silk & Brown’s (2008) conclusion that LRC and LRE shape BSRs.

The results of our study are not conclusive. We hope that future studies of ringtailed lemurs will provide valuable data for the further evaluation of socioecological hypotheses concerning the evolution of BSR in primates.

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